

## Interactions between zooplankton and phytoplankton profiles in the eastern tropical Pacific Ocean

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**Abstract**—Data from 86 detailed zooplankton profiles taken during the EASTROPAC cruises of 1967 to 1968 have enabled a first-order description to be made of zooplankton distribution in the upper 1000 m of the water column in relation to density, light, oxygen, and phytoplankton. A layer of abundant epiplankton contains a subsurface maximum that tends to coincide with the bottom of the mixed layer and with the depth of maximum carbon fixation, but lies above the chlorophyll-*a* maximum. Zooplankton abundance declines sharply downwards across the pycnocline, forming a discontinuity between the epiplankton and the low-biomass plankton below. Coincident with the deep sonic scattering layers are diurnal layers of migrant interzonal species which rise at night into the epiplankton. Major regional differences are caused by the shoaling of the pycnocline at the equatorial divergence, and the very deep pycnocline of the southern gyral region. An hypothesis, based upon the EASTROPAC data, is stated: that the form of phytoplankton profiles, in periods or regions of stable production, may be primarily determined by a depth-differential in herbivore grazing pressure, rather than by differential cell-sinking rates as is suggested in classical production models.

### INTRODUCTION

ZOOPLANKTON abundance in low latitudes appears to be greatest in a relatively shallow layer which is separated from water containing much less zooplankton at some depth between 100 and 300 m. VINOGRADOV (1968) reports many zooplankton profiles for low Pacific latitudes in which plankton abundance decreases by about an order of magnitude between the surface and 1000 m to a very low biomass, which is itself reduced by another order of magnitude only between 3000 and 5000 m. It is also evident from these profiles that biomass in the upper kilometre of the water column contains a discontinuity at some depth above 500 m, at which most of the decrease occurs. Such a discontinuity may occur elsewhere in the oceans, though its depth varies considerably (e.g. FOXTON, 1956; GRICE and HULSEMANN, 1965).

It is predictable that zooplankton profiles should contain a degree of complexity to match what is well known to occur in pumped phytoplankton profiles; however, because of the restrictions imposed by opening-closing nets for zooplankton collection, only very rarely have zoo-

plankton profiles been obtained of comparable resolution to profiles of phytoplankton and its related variables, which can be obtained by pumps with much less expenditure of ship-time; commonly, only about five levels are sampled down to about 500 m with opening-closing nets (e.g. VINOGRADOV, 1968). When higher resolution has been obtained, as with the new series of RMT1 and RMT8 nets (BAKER, CLARKE and HARRIS, 1973), several hours are required to obtain a single profile, during which period vertical migration may to some extent occur even if twilight is avoided, and it is usually impossible to work many such stations during one cruise or survey.

For these reasons, the number of stations for which we have zooplankton profiles of high resolution is relatively small, and although the details of plant and animal profiles must, in fact, be causally matched by the processes of grazing and regeneration of nutrient salts, we have not advanced much farther in our interpretation of these relations than the models of RILEY, STOMMEL and BUMPUS (1949) and of STEELE and YENTSCH

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(1960) in which grazing was considered to be a uniform factor throughout the euphotic zone—which it clearly is not.

The EASTROPAC expeditions in 1967 to 1968 were designed to monitor seasonal change in a large part of the eastern tropical Pacific Ocean, between about 20°N and 20°S; cruise and station numbers used in the present paper are the same as presented in the EASTROPAC Atlases (LOVE, 1971). Zooplankton hauls with multiple serial plankton samples (LONGHURST, REITH, SEIBERT and BOWER, 1966), or Longhurst-Hardy Plankton Recorders (LHPR's), as they have come to be called, were included in standard EASTROPAC station procedures together with profiles of plant pigments, carbon fixation, inorganic nutrients, oxygen, transparency and physical variables; all station and data processing procedures are described by LOVE (1971). These data enable us to examine, over a very large area of the ocean and over all seasons, the relationships between profiles of zooplankton and other variables in the upper kilometre of the water column.

For the purposes of this investigation it was assumed that net-caught zooplankton were predominantly herbivores (p. 749); it was further assumed, except in some special cases discussed separately, that carnivores would aggregate, in general, at similar depths to their herbivore prey.

#### DATA ACQUISITION

The zooplankton profiles were taken with 0.5 m<sup>2</sup> LHPR equipment, fitted with 0.3 mm nylon filtering gauze. Successful profiles were obtained at 86 stations (Fig. 1) during four cruises of the *David Starr Jordan*, as follows:

##### EASTROPAC cruise

- 12—February–March 1967—32 stations
- 30—June–July 1967—20 stations
- 60—December–January 1967-68—21 stations
- 76—March 1968—13 stations.

All stations were worked within about one hour of midday and midnight in order to sample only when diel migrants were at their most stable in respect of depth levels, and to avoid the dusk and dawn periods of relatively very rapid vertical movement. Even though, as ROE (1974) has

recently confirmed, some vertical shifts occur during the periods of full daylight and darkness, midday and midnight levels effectively represent the depth at which diel migrants spend most of their time.

The standard LHPR haul comprised a single oblique profile to the surface; the gear was sunk as rapidly as possible, usually in little more than 5 min, until it was judged that it had reached 500 m, at which depth it was held for 2 min to stabilize itself. It was then hauled slowly and obliquely to the surface with about 50 sampling periods, each of 30-s duration, giving an average sampling depth interval of 9.3 m and a total hauling time of about 30 min. There were 73 such standard stations on cruises 12, 30 and 60, which were found subsequently to have varied from 200 to 700 m in sampling depth, though half fell within the range 450 to 500 m. In addition, on cruise 76 there were 10 special shallow hauls designed to give greater resolution within the mixed layer; these had an average sampling depth interval of only 2.5 m between the surface and depths of 150 to 300 m. Finally, on the same cruise three special deep hauls from 1000 m were worked successfully.

The total number of individual plankton samples from these 86 stations was 3886, each representing about 10 m<sup>3</sup> filtered; the actual amount filtered and the sampling depth intervals were recorded for each sample by the instrument, and used to normalize the data. The LHPR equipment had no bridles in front of the net aperture and was coloured black: these measures appear to have so reduced net-avoidance by zooplankters that no consistent day/night ratio could be detected in numbers of organisms per cubic metre, and the problems discussed by BRINTON (1967) were apparently not important.

The plankton nets and recorder were carefully examined on recovery; whenever serious hang-up of organisms on the nets was found to have occurred, the haul was rejected, as were hauls in which subsequent sample editing showed that entrainment of specimens in the recorder had occurred. Rejected hauls were about 10% of all hauls taken, and are not listed here.

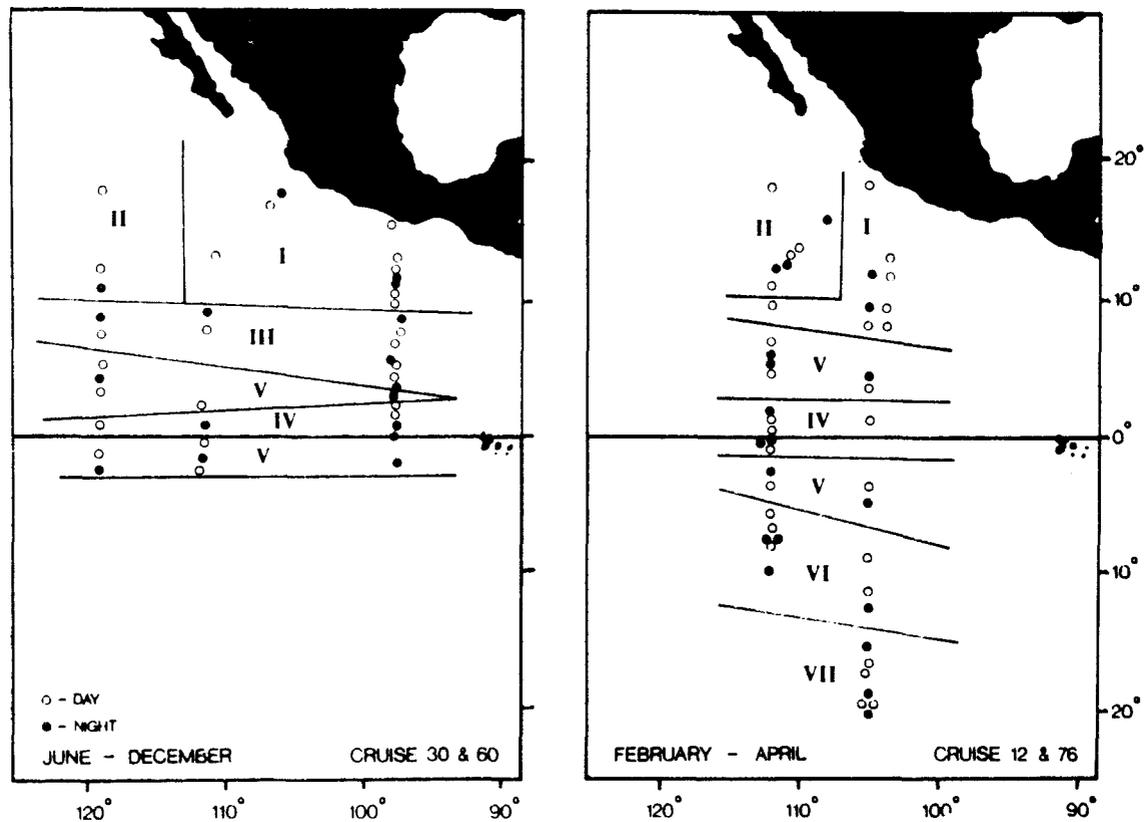


Fig. 1. Location of LHPR profiles and allocation of stations to oceanographic regions I to VII; open circles—midday stations, closed circles—midnight stations.

The samples were subsequently sorted into 18 major categories (all coelenterates, all copepods, chaetognaths, molluscs, cladocera, etc.) and 18 minor categories including some genera (e.g. *Euchaeta*, *Eucalanus*, *Candacia*), some artificial groups (e.g. large and small species of *Pleuromamma*) and some single species (e.g. *Rhincalanus nasutus*, *R. cornutus*, *Euphausia diomediae*, *E. gibboides*). Twenty-one profiles from cruise 12 were sorted for six species of *Clausocalanus* as part of a different investigation: these data are included in those considered here. Biomass, expressed as dry weight in  $\text{mg m}^{-3}$ , was computed from volumetric measurements made on each sub-sample using factors experimentally derived for 10 categories of zooplankton composition as sampled by the auxiliary net fitted to

the LHPR (LONGHURST, REITH, SEIBERT and BOWER, 1966); each sub-sample was allocated to the zooplankton composition category it most closely resembled, to determine the appropriate conversion factor.

#### THE EASTROPAC AREA

The EASTROPAC area comprises the eastern tropical Pacific Ocean from 20°N to 20°S and from the American continent out to 120°W. The station lines on which LHPR profiles were obtained run north-south between 98 and 118°W, so as to form transects normal to the zonal current system (Fig. 1). Rather than group the profiles within rectangles based on latitude and longitude in the same way as BLACKBURN, LAURS, OWEN and ZEITSCHL (1970), in their

studies of the multiple correlation of biotic and abiotic variables in the horizontal plane, I have chosen instead to identify a series of oceanographic regions within the EASTROPAC area, each with consistent and definable characteristics, and the zooplankton profiles have been pooled accordingly.

Examination of all available station data, mostly as presented in the EASTROPAC atlases, indicated that there were seven such regimes characterized by the vertical variability of properties known to influence the vertical distribution of zooplankton. The areal extent of these regimes and the allocation of zooplankton profiles to them is indicated in Fig. 1; they have the following characteristics:

*Region I.* A triangular area bounded by the Mexican coast and by  $10^{\circ}\text{N}$  and  $110^{\circ}\text{W}$ , of variable currents, the surface water originating in the north from January to May after which, with the seasonal development of the north equatorial counter-current in Region III, the Costa Rica Current brings equatorial surface water inside California Current water which it entirely replaces in the area until August to October when a southerly component from the California Current again invades the area. Surface temperatures are higher here than in the rest of the EASTROPAC area, frequently exceeding  $29^{\circ}\text{C}$  from April to September; mixed layer depths are always moderate so that the bottom of the isothermal layer, of D1 (WYRTKI, 1964), lies between 20 and 50 m, the thermocline having a complex topography with much seasonal and areal variation. In the second half of the EASTROPAC year D1 was shoaler (20 m) and mixed layer temperatures warmer ( $28$  to  $29^{\circ}\text{C}$ ) than in February–March (50 m,  $26$  to  $28^{\circ}\text{C}$ ), and northward coastal flow after June was associated with replacement of a thermocline ridge 300 to 400 miles off the coast by a trough, from which D1 shoaled towards the coast. This region overlies the greatest oxygen deficiencies in the North Pacific, and values below  $0.25\text{ ml l}^{-1}$  occur within the oxygen minimal layer.

*Region II.* To the west and southwest of the first area the extension of the California Current

as the north equatorial current dominates surface flow throughout the year; temperatures are lower, and vary more during the year than closer to the coast, from  $21$  to  $26^{\circ}\text{C}$  seasonally, with the effects of the northern hemisphere winter and of coastal upwelling at Baja California. The oxygen minimum tends to have slightly higher minimal values ( $0.25$  to  $0.50\text{ ml l}^{-1}$ ) than in Region I, and the mixed layer tends to be deeper, so that D1 is typically greater than 50 m.

*Region III.* The north equatorial counter-current traverses the northern part of the study area between  $5$  and  $10^{\circ}\text{N}$  except between February and May, when it does not extend east of about  $120^{\circ}\text{W}$  at the surface, though it is detectable in the thermocline topography farther east at this time. The occurrence of this flow from the west is indicated in the slope of the thermocline downwards towards the south, from a zonal ridge at  $10$  to  $12^{\circ}\text{N}$  along the northern boundary of the current to a zonal trough centered at about  $4^{\circ}\text{N}$ , which indicates its southern boundary. Thus, D1 varies from 90 m in the south to only 20 m in the north, and there is considerably greater variation in its depth during any one cruise than there is between seasonal means. Profiles were obtained from the north equatorial counter-current, however, only in the second half of the year and these showed D1 to be much shoaler than in Region I north of the thermocline ridge at  $10$  to  $12^{\circ}\text{N}$ . The oxygen minimal layer includes values no lower than  $0.5\text{ ml l}^{-1}$ , and ranges from 300 to 500 m in thickness.

*Region IV.* About  $2^{\circ}$  north and south of the equator the water column is very strongly influenced by seasonal equatorial Ekman divergence and by the shallow, eastward-flowing equatorial under-current; the latter lies close to the surface, its core being scarcely deeper than 50 m, and its latitudinal extent and relative velocity indicated by the equatorial troughing of isotherms in the lower part of the thermocline ( $12$  to  $20^{\circ}\text{C}$ , Fig. 2) and by the location there of a salinity core ( $34.9$  to  $35.2\text{‰}$ ).

Equatorial divergence causes the thermocline to approach the surface so closely that the mixed layer may be extremely shoal, commonly less than

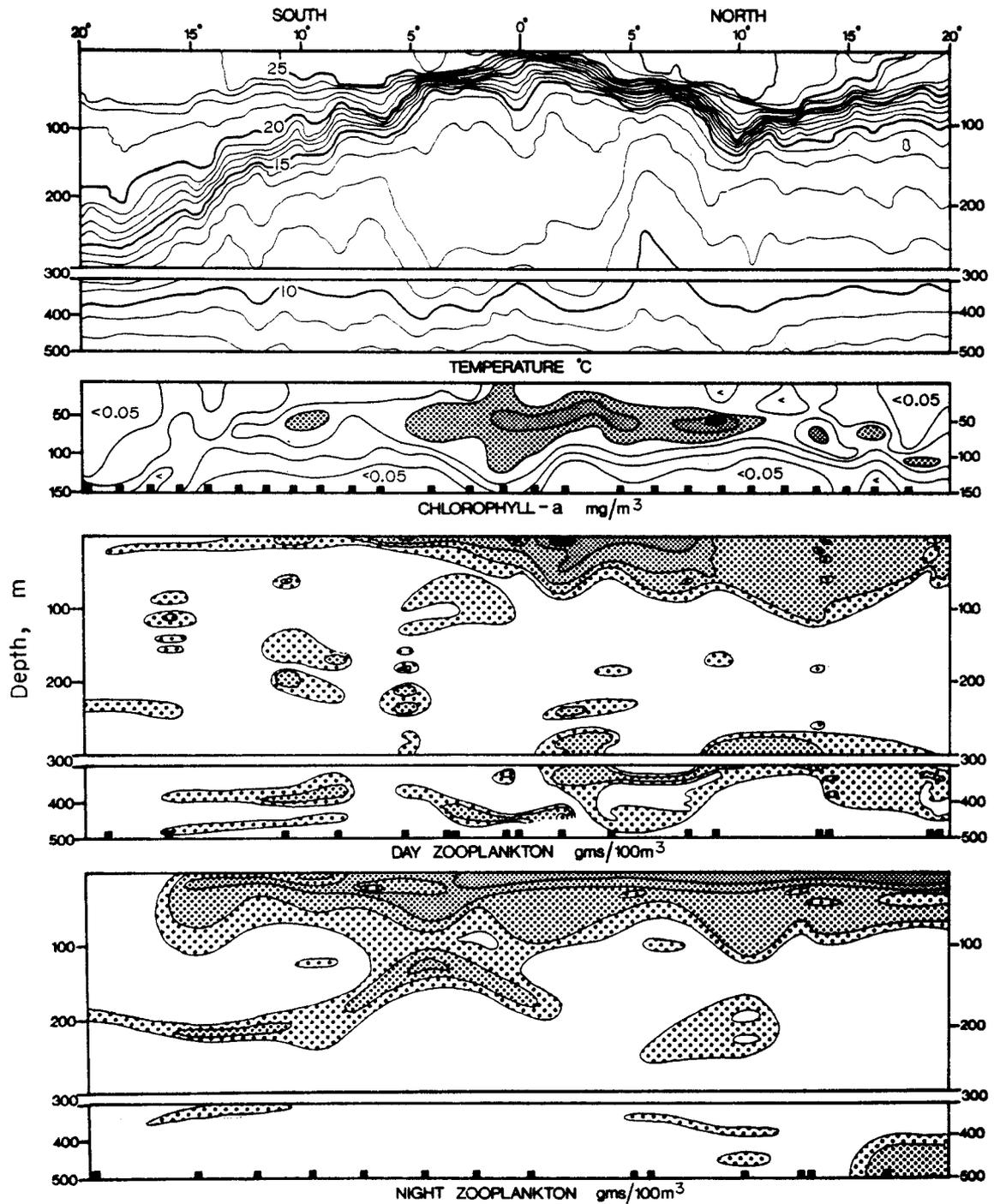


Fig. 2. Sections along EASTROPAC transects at 110°W; the symbols along the baselines indicate station positions. Chlorophyll-*a* is contoured at seven levels, from  $> 0.4$  to  $< 0.05$   $\text{mg m}^{-3}$ ; zooplankton at six levels, from  $> 2000$  to  $< 100$   $\text{g (100 m}^3\text{)}^{-1}$ .

10 m deep. From May until about November this process appears to surface the equatorial under-current (CROMWELL, MONTGOMERY and STROUP, 1954; JONES, 1969) so that the permanent tropical mixed layer is obliterated, probably assisted by turbulent diffusion (WILLIAMS and GIBSON, 1974), resulting in a deeper homogeneous layer ( $\leq 40$  m), though at considerably lower temperatures ( $\leq 20^\circ\text{C}$ ) than earlier in the year. This situation was established at some stations in June and July, 1967 (cruise 30) and remained so throughout the rest of the year; at all Region IV stations in December (cruise 60) the primary thermocline had been eliminated and a cool mixed layer ( $22^\circ\text{C}$ ) of rather variable depth was established. By February 1968 (cruise 76) the tropical mixed layer was re-established, though it was everywhere very shoal.

Consequent upon the general shoaling of the isotherms at the equator, the  $\text{O}_2$  minimum layer, which has minimum values greater than  $0.50 \text{ ml l}^{-1}$ , lies very shoal.

*Region V.* Throughout the year, equatorial surface water is transported westwards by the south equatorial current broadly over the EASTROPAC area south of about  $9^\circ\text{N}$  and it is within this westward zonal drift that Region IV outlined above is embedded as a very narrow equatorial ribbon.

Region V is recognized as the region of strongest zonal flow of the south equatorial current, its northern extent limited by the southern boundary of the north equatorial counter-current at the  $4^\circ\text{N}$  thermocline trough or by a broad zone of convergence at  $7$  to  $9^\circ\text{N}$  when the north equatorial counter-current is absent. South of the equator, the permanent thermocline deepens southwards throughout the EASTROPAC region. An interruption in this slope by a region in which southward shoaling of the summer thermocline occurs is associated with a weak, subsurface south equatorial counter-current (TSUCHIYA, 1974); the southern edge of this current, where the mixed layer deepens again southwards, is taken as the limit of Region V.

This region has a mixed layer with relatively strong small-scale thermal layering at many

stations both north and south of the equatorial divergence, this being especially true of those with a deeper D1. Variations in thermocline depth appear to contain no seasonal component and to be due to the relative instability of the upper 100 m here compared, in particular, with Region I.

*Region VI.* From about  $7$  to  $9^\circ\text{S}$ , the velocity of the south equatorial current slackens, the surface water mass changes its characteristics, and a summer thermocline occurs; this is a regime of gentle westward drift, increasing mixed layer depths and increasingly high values in the  $\text{O}_2$  minimum towards the south. A number of distributions of planktonic animals and bathypelagic fish (AHLSTROM, 1971; MCGOWAN, 1971) appear to coincide with the boundary between Regions V and VI.

*Region VII.* In the extreme south of the area, from about  $15$  to  $16^\circ\text{S}$ , the south Pacific central water mass is evident in the water column, being principally indicated by a salinity maximum which progressively strengthens and deepens towards the south, though the separation from Region VI is not very well defined. D1 increases progressively southwards, as does the summer mixed layer above it, and reaches 250 m at  $20^\circ\text{S}$ . Thermocline gradients are slight and only exceptionally is there no mixed layer temperature stratification, even above the summer thermocline. There are very low standing crops of all biota, and deepening of features of the phytoplankton profile, especially south of  $14^\circ\text{S}$  where the chlorophyll-*a* maximum occurs deeper than 200 m at some stations; oxygen values lower than  $1.0 \text{ ml l}^{-1}$  do not normally occur in the water column.

#### GENERAL FEATURES OF THE ZOOPLANKTON PROFILES

Zooplankton profiles for biomass, total numbers of organisms and for all sorted categories were computer-generated for each station; examination of the general profiles for biomass and numbers immediately indicated a high degree of commonality among their general features, especially when the profiles were pooled regionally. Copepods, being more numerous in all profiles by factors varying between 7 and 10,

together with chaetognaths and euphausiids, whose biomass is also very important, dominated the form of the profile for biomass and number of organisms.

Three main features (Figs. 3 and 4) can be seen in most profiles and are defined below: an *epiplankton*, a *planktostad*, and *discrete layers* within the planktostad.

From the surface down to depths ranging from

50 to 150 m in all except nine of the 86 profiles of biomass and total numbers there is a layer of abundant zooplankton having dry weight values ranging from 1 to 1000 mg m<sup>-3</sup>, and with numbers of all organisms frequently as high as 900 m<sup>-3</sup> and rarely below 100 m<sup>-3</sup>. It is convenient to apply the term *epiplankton* to this layer, following FOWLER (1898), VINOGRADOV (1968) and others.

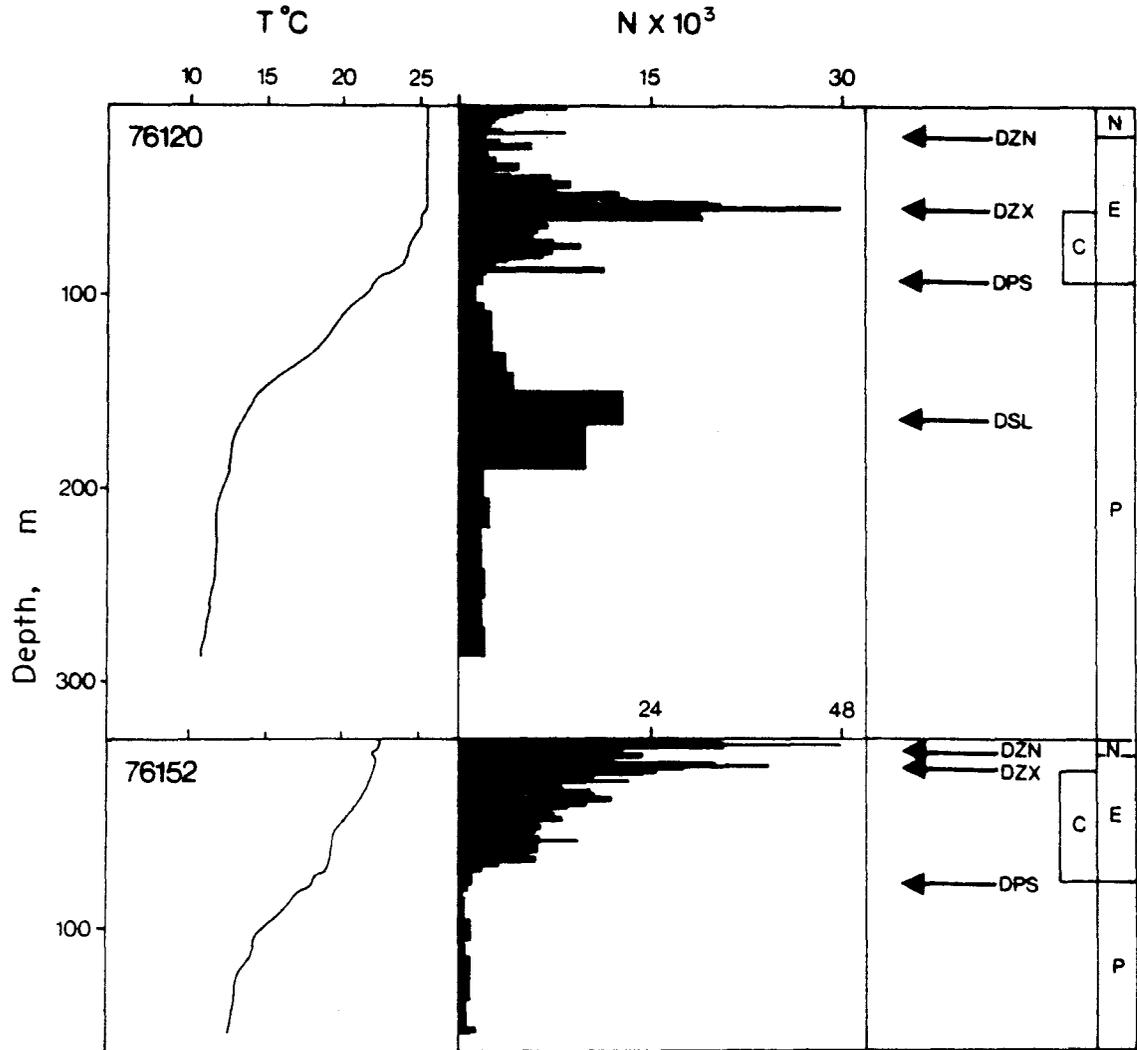


Fig. 3. Two exemplary shallow daytime profiles (total organisms 100 m<sup>-3</sup>) to demonstrate their principal features; N = neuston, E = epiplankton, C = planktostad, P = planktostad. Remainder of notation as in text, p. 737.

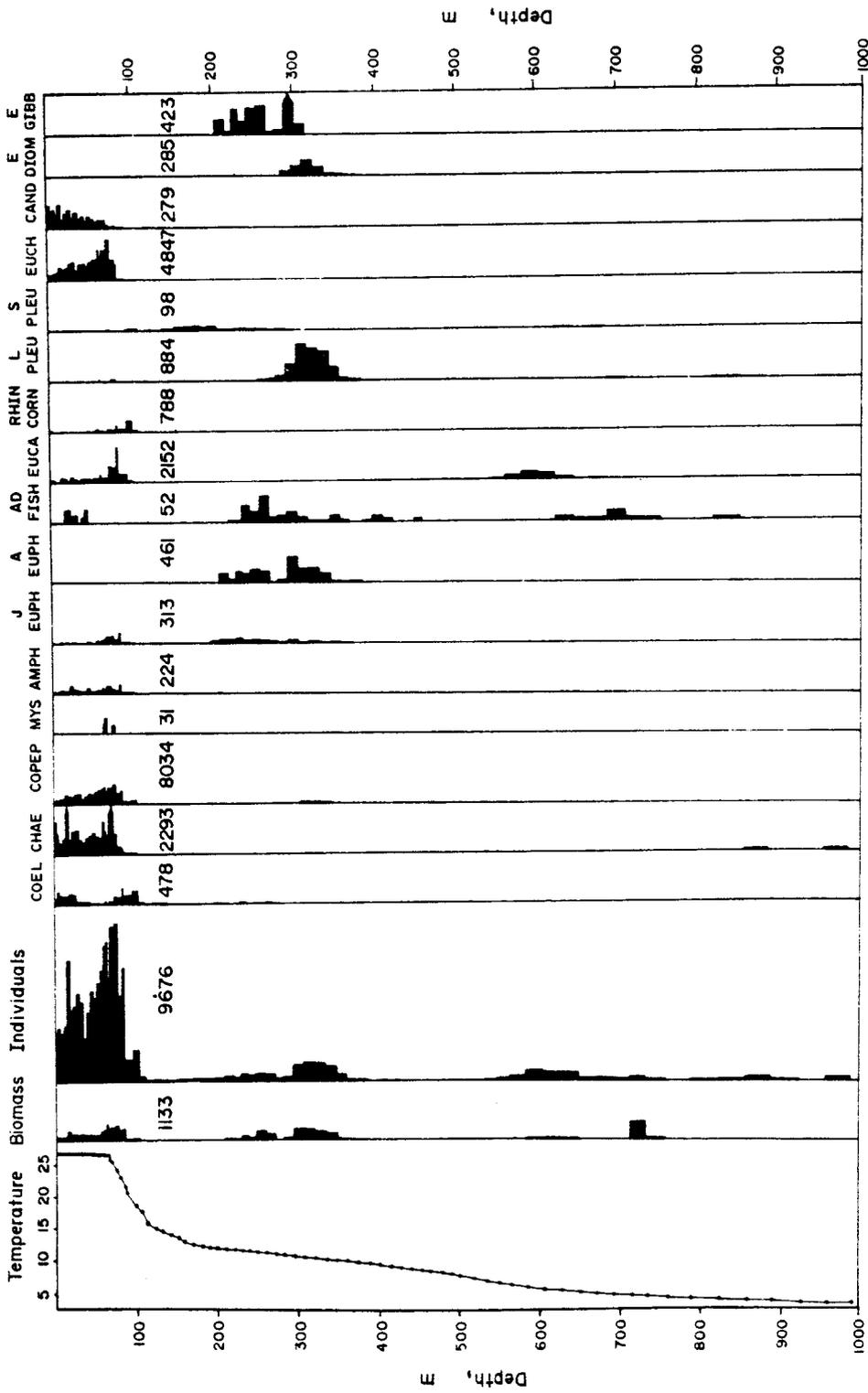


Fig. 4. Special deep daytime profile (76202) at 14°N to show layering of taxa; in this computer-derived plot the horizontal scales are arbitrary; against each histogram are indicated the maximum numbers per 100 m³ or maximal biomass in g (100 m³)⁻¹ reached in that profile. Abbreviations are of major and minor sorted categories, defined in text, p. 731.

The lower limit of the epiplankton is usually well defined at the bottom of a depth zone across which plankton abundance usually decreases by 100 to 1000 organisms  $m^{-3}$  per meter of depth increase, or about 2 to 10% of the epiplankton average value per meter and which can conveniently be described as a *planktocline*;\* in day profiles a *zooplankton minimum* frequently lies at 10 to 25 m separating a layer of more abundant near-surface zooplankton from the main body of the epiplankton below. A major faunistic boundary occurs at the bottom of the epiplankton, which forms the lower limit for many species and genera of copepods, for all cladocera, for most polychaetes, and for some decapods.

Below the planktocline, plankton biomass and numbers are from one to several orders of magnitude lower (0.1 to 1.0  $mg\ m^{-3}$  and *ca.* 10 individuals  $m^{-3}$ ) and change very little with increasing depth to at least 1000 m. This can therefore be described as a *planktostad*,\* which continues downwards for several thousand meters (e.g. VINOGRADOV, 1968: pp. 188 to 189), and within which rates of change are so small as to be unquantifiable in the present data.

Single interzonal species or groups of species occur both within the epiplankton by night and the planktostad by day, but are more prominent within the latter, where they form important discrete layers; these may, or may not, coincide with *deep scattering layers* (DSL), they extend throughout the sampled depth range of the planktostad, and they usually represent daytime populations of diel vertical migrants, or upper interzonal species in the sense of VINOGRADOV (1968, p. 51).

The biomass of such depth-discrete layers may approach 5  $mg\ m^{-3}$ , and may be greater than the planktostad background by at least an order of magnitude, and also they may be extremely thin (5 to 10 m is not unusual) in the vertical sense. Such layers have previously been reported in LHPR profiles in the California Current (LONGHURST, 1967), the North Sea (KINZER, 1970), the North Pacific (BARRACLOUGH, LEBRASSEUR and KENNEDY, 1969) and the North Atlantic (Williams, personal communication)

and, from our general knowledge of the oceanic distributions of DSLs, are probably a common feature in many parts of the ocean.

From examinations of the profiles of biomass and of total individuals, depths were assigned to the major features of the profiles; in almost every case the two profiles agreed but, when they did not, the data derived from the biomass profile were discarded:

DPS —depth of the bottom of the epiplankton, defined by the planktocline–planktostad boundary.

DZX—depth of the subsurface zooplankton maximum that may occur within the epiplankton.

DZN—depth of the subsurface zooplankton minimum that frequently separates the main body of the epiplankton from a near-surface layer, having its own maximum abundance within 10 to 15 m of the surface.

In addition, from the temperature record made by LHPR for each profile and from associated EASTROPAC station data, the depths of a number of related environmental parameters were determined:

D1 —the depth of the base of the mixed layer, from STD casts;

D2 —the depth of the base of the thermocline (WYRTKI, 1964), also from STD casts;

DE —the depth of the bottom of the euphotic zone, at the 1% incident light level, determined from Secchi disc extinction depths by appropriate conversions (LOVE, 1971);

DCLX—the depth at which the subsurface chlorophyll-*a* maximum occurs (YENTSCH, 1965), determined from Lexan bottle casts (LOVE, 1971);

DCX —the depth at which the maximal rate of uptake of  $^{14}C$  was measured in

\*The general suffixes—cline and stad—used in oceanography to denote the presence or the absence, respectively, of a gradient (as in *thermo-*, *halo-*, *pycno-*, *oxy-*, etc.) are here used for the same purpose, as a matter of convenience, in relation to plankton.

simulated *in situ* primary production experiments (LOVE, 1971);

DPHX—the depth of the subsurface maximum of phaeopigment concentration, from the same bottle samples as used for chlorophyll-*a* determination.

Finally, though not used subsequently in the formal correlation programme, information was extracted on:

DCLN—the depth of the bottom of the major chlorophyll-*a* maximum where values fell to below a value of 0.05 mg m<sup>-3</sup>;

DON, DNOX—respectively, the depths of the oxygen minimal layer, and of the shallow NO<sub>2</sub> maximum, determined from reversing bottle casts.

The 19 sets of profiles of specially sorted taxa were then examined and depths derived for major layers (or for maximum abundance in unlayered taxa) both within the planktostad and the epiplankton (Table 1). In the case of diel migrant taxa, separation was made between depths of the main migratory parts of the population and the depths of the residual, non-migrating layers which are a characteristic feature of such taxa (e.g. LONGHURST, 1967).

The data derived from the general profiles were stratified by time (day/night), season (cruise) and regionally, and an analysis of variance between the strata was performed, as was a linear regression in all unstratified permutations of two of the eight variables (Table 2). A stratified table of differences

Table 1. Mean depths of variables, stratified by region;  $\bar{X}$  D-N is the mean difference between day and night depths.

Region	Zooplankton			Phytoplankton			Environment			
	DPS	DZX	DCX	DCLX	DCLN	DPHX	D1	D2	DE	DNO2
I	98.2	39.0	25.0	49.5	107.0	81.9	47.8	119.7	65.6	70.4
II	82.5	41.3	30.0	70.0	105.0	95.0	47.5	120.0	84.3	-
III	89.4	31.1	29.3	49.4	112.0	75.0	30.9	93.6	86.1	64.2
IV	77.6	11.9	22.9	38.4	108.0	66.6	25.2	98.9	66.8	51.6
V	89.0	25.7	31.5	52.8	122.0	76.8	36.1	113.3	64.3	58.9
VI	80.0	60.7	22.1	58.6	130.0	96.4	51.6	195.0	56.3	111.4
VII	-	35.0	39.2	120.8	150.0	146.7	68.3	251.7	77.2	-
$\bar{X}$	88.5 (±2.3)	30.8 (±3.2)	27.6 (±1.3)	55.3 (±1.7)	119.0 (±2.8)	84.0 (±3.0)	37.9 (±1.6)	126.6 (±4.1)	66.7 (±1.6)	71.3 (±3.1)
$\bar{X}$ D-N	+7.7	+10.4	-	+3.5	-	-6.0	+12.1	+4.7	-	-

Table 2. Correlation coefficients ( $r$ ) of linear regressions, all permutations of two of eight selected variables.

	D1	D2	DE	DCLX	DCX	DPHX	DPS
D1							
D2	+0.626***						
DE	+0.161 NS	+0.178 NS					
DCLX	+0.555***	+0.666***	+0.413***				
DCX	+0.209*	+0.218*	+0.444***	+0.299**			
DPHX	+0.115 NS	+0.314**	+0.057 NS	+0.262*	-0.045 NS		
DPS	+0.338**	+0.053 NS	+0.204 NS	+0.342**	+0.286*	-0.110 NS	
DZX	+0.396***	+0.415***	+0.065 NS	+0.294**	+0.148 NS	+0.066 NS	+0.482***

NS—not significant ( $P > 0.05$ ). \*—just significant ( $P 0.01-0.05$ ), \*\*—significant ( $P 0.001-0.01$ ), \*\*\*—very significant ( $P < 0.001$ ).

Table 3. Depth differences (m) stratified by time and region, between DZX, DPS and six environmental variables. Abbreviations as in text and Table 2. Stated significance is that between depths of indicated pairs of variables.

	DAY		NIGHT		DAY + NIGHT
	I-III	IV, V	I-III	IV, V	I-VII
DZX = D1	+3 NS	-20 **	-6 NS	-3 NS	-5.0 ± 3.3 NS
= D2	-70 ***	-88 ***	-89 ***	-86 ***	-88.1 ± 4.3 ***
= DE	-29 ***	-40 ***	-47 ***	-63 ***	-35.4 ± 3.7 ***
= DCLX	-9 *	-28 ***	-21 ***	-26 ***	-20.5 ± 3.5 ***
= DCX	+18 **	-11 **	+2 NS	-7 NS	+3.4 ± 3.1 NS
= DPHX	-38 ***	-49 ***	-55 ***	-57 ***	-49.1 ± 4.4 ***
DPS = D1	+58 ***	+47 ***	+56 ***	+57 ***	+53.9 ± 2.5 ***
= D2	-15 **	+20 **	-24 **	-29 **	-25.8 ± 4.0 ***
= DE	+26 ***	+27 ***	+16 *	+19 *	+22.6 ± 2.5 ***
= DCLX	+47 ***	+38 ***	+41 ***	+37 ***	+40.0 ± 2.4 ***
= DCX	+69 ***	+56 ***	+63 ***	+55 ***	+61.1 ± 2.4 ***
= DPHX	+18 **	+17 *	+7 NS	+7 NS	+11.1 ± 4.0 **

(Table 3) between DPS and DZX and the other six variables was constructed and each difference subjected to analysis of variance and of significance.

These processed data were then used as the basis of an examination of the relationship between the variables and of possible reasons for the observed form of the zooplankton profiles.

#### VERTICAL EXTENT OF EPIPLANKTON

Preliminary examination of the general profiles showed that while the general features associated with the epiplankton could be recognized at nearly every station, there was great variability in detail, principally concerning the depth at which features occurred; it was also evident that the variability was rather strongly linked with the regional pooling of the stations. It is to be supposed that the planktocline, the depth at which the vertical extent of the abundant epiplankton is limited, would be the result of the presence of a constraint in the physical environment or by the insufficiency of the food supply below such depth; these possibilities are now explored.

#### Density and temperature

In tropical seas, temperature is a practical

indicator of density of sufficient precision for present purposes and so we may define the pycnocline by D1 and D2, or as coincident with the thermocline.

Because of this relatively direct relationship between density and temperature, the lower part of the pycnocline coincided with the same groups of isotherms over the whole region; the data suggest that DPS and the 14°C isotherm coincide rather frequently, though this is most unlikely to be in any sense a depth-limiting factor in the distribution of the epiplankton, and the possibility was not investigated formally.

Analysis of the depth differences DPS-D1 and DPS-D2 showed that DPS usually occurred in the lower part of the pycnocline, and there was no case in which it occurred shoaler than D1, or within the mixed layer; in only 16 of the 75 profiles at which DPS could be identified did it occur deeper than D2. The mean depth differences were very significant in each case:

$$\text{DPS} = \text{D1} + 54 \pm 2.5 \text{ m } (P < 0.001)$$

$$\text{DPS} = \text{D2} - 26 \pm 4.0 \text{ m } (P < 0.001).$$

Significance at this level was maintained for all strata (time, season and region), and the linear regression DPS/D1 (D1 being the more satisfactorily determined parameter of the thermocline) showed significant covariance ( $r = 0.338$ ;  $P$  0.001 to 0.01) for all data strata.

An examination of the 16 exceptions showed that in 11 stations at which the epiplankton appeared to extend below the base of the thermocline (i.e. where  $\text{DPS} > \text{D2}$ ), the difference was by a margin of only 2 to 17 m, possibly to be accounted for by the imprecision of the quantification of D2 from the temperature profiles.

As for the remaining exceptions, two stations (30215 and 60257) lay within the equatorial divergence cell in Region IV to the west of the Galapagos Islands where the thermocline had surfaced and D2 was relatively very shoal, at only 38 m in the case of 30215; two other stations (30246 and 60284) lay on the southern slope of the Costa Rica dome, having mixed layer depths less than 20 m and rather shoal values for D2 of  $\leq 60$  m (regional means were 92 to 117 m).

At the final station 76120, at which DPS apparently lay 101 m below D2, there was a deep migrating layer lying unusually shoal, and inseparable from the epiplankton, so DPS must have been calculated in error.

The eleven stations at which DPS could not be identified were, with a single exception, all at the extreme south of the EASTROPAC area where D1 and D2, but especially the latter, lie very deep (p. 734 and Table 1). In Regions VI and VII, DPS could be identified only at night stations in Region VI; at day stations in VI, and both day and night stations in VII, it was not possible to identify a planktocline below an abundant layer of epiplankton. These profiles suggest that in these regions of very deep pycnoclines it is only at night, as a result of the crepuscular rise of diel migrants that a planktocline is formed, and that even this does not occur south of about 15°S. Unfortunately, there were too few stations in Regions VI and VII to analyse statistically the relationship between DPS and density or temperature.

The single station (30233) in low latitudes at which DPS could not be identified was situated in an area of dynamic upwelling to the west of the Galapagos Islands, and no explanation for this anomaly is evident.

#### *Light*

EASTROPAC data on light penetration are derived from 30-cm Secchi disc extinction depths and therefore are available only for day stations. Reflecting the fact that the only important source of turbidity in this area is pelagic biological production, light penetration is closely correlated with the depth of the layer of abundant plant cells (Table 2). The mean value of DPS is deeper by  $23 \pm 2.5$  m than DE ( $P < 0.001$ ), and although the range of variability in this difference is not great, the attempt to demonstrate linear correlation fails ( $r = 0.204$ ,  $P > 0.05$ ), and it seems improbable that DPS is primarily determined by the light regime; even though DPS shows a very minor diel depth fluctuation, which has the correct sign to be caused by normal vertical migration patterns, the day-night difference (+ 7.7 m,

Table 1) is not significantly different from zero ( $P > 0.10$ ).

#### *Oxygen*

The eastern Pacific oxygen-deficient layer is shoal and very strongly developed in Region I, to the southwest of Baja California and the Mexican coast (BRANDHORST, 1959; WYRTKI, 1962). Earlier studies in this layer (LONGHURST, 1967) have shown that oxygen levels only below  $0.2 \text{ ml l}^{-1}$  may constrain the distribution of interzonal migrant zooplankton. This oxygen isopleth was as shoal as 75 m at some stations in Region I and at four of these (12006, 12030, 30250 and 30258) DPS was as much as 30 m deeper, and well into water with very high oxygen deficiency. Such observations suggest that oxygen plays a negligible role in determining the depth distribution of the epiplankton. Moreover, in most of the EASTROPAC profiles, the  $0.2 \text{ ml l}^{-1}$  isopleth lay much deeper than DPS.

#### *Phytoplankton*

Of the 86 LHRP stations, there were 77 at which profiles of chlorophyll-*a* and phaeopigments were also obtained and 48 daytime stations at which profiles of 14-C uptake rate were taken. These three parameters of the phytoplankton had a rather constant relationship: the subsurface chlorophyll maximum was underlain by a deeper phaeophytin maximum, while the depth of maximum gross production rate lay shoaler. At 11 southerly stations the phytoplankton sampling was not carried sufficiently far down to reach the chlorophyll maximum which lay very deep indeed ( $> 125$  m) at some stations in Regions VI and VII.

Since the simplest hypothesis relating the depths of abundance of animals and plants is that zooplankton do not exist in abundance below the depth at which a significant standing stock of phytoplankton occurs the relations of DCLN with DPS were examined first.

DCLN lay between 105 and 115 m right across Regions I to V, showing remarkably little variance (Table 1): it did not appear to react to shoaling of D2 in very low latitudes in Region IV and deepened less strongly than D2 in the

southernmost Regions VI and VII. Because of its relation with D2, therefore, DPS always lay shoaler than DCLN by 25 to 50 m in Regions II to VII; only in Region I, with its very well-defined and relatively shoal mixed layer, was there a closer correspondence between D2, DCLN and DPS. The lack of better correspondence between DPS and DCLN might indicate that an incorrect chlorophyll value was selected to define the latter; however, a value which would give a better match in Regions I to V (say the  $0.1 \text{ mg m}^{-3}$  isopleth) gives a rather poor match in the southernmost regimes, as would a value based upon a percentage of the maximal chlorophyll value.

As expected, the formal analysis of difference and correlation confirmed that DPS lay significantly deeper than DCLX and DCX:

$$\text{DPS} = \text{DCLX} + 40 \text{ m} \pm 2.4 \text{ m} \quad (P < 0.001)$$

$\text{DPS} = \text{DCX} + 61 \text{ m} \pm 2.4 \text{ m} \quad (P < 0.001)$ , and although the linear regressions indicate some covariance, this is not very significant (for DPS/DCLX,  $r = 0.342$ ;  $P$  0.001 to 0.01; for DPS/DCX,  $r = 0.286$ ;  $P$  0.01 to 0.05).

Taken together, the evidence on density, light, oxygen and phytoplankton indicates that the lower limit of the euplankton is usually determined by the lower part of the thermocline, though not by its deepest isotherms and isopycnals, and that it occurs in a rather loose association with the lower limit of chlorophyll-rich water; it appears to be unrelated to light penetration or to oxygen content.

#### DEPTH CONTROL OF EPIPLANKTON MAXIMA

Within the euplankton, DZX could be identified in 80 of the 86 profiles of biomass, of total numbers of organisms, of total copepods and of total chaetognaths. There is a greater diel variation in DZX than in DPS, and the regional mean day-night differences range from 6.8 (Region IV) to 45.0 m (Region VI), and because DZX is much shoaler than DPS, its day-night differences are a much higher percentage of its day depth, regional means ranging from 30 to 58%.

Diel variation in the depth of maximum plankton aggregation reflects two different processes: the nocturnal rise (or sinking) of the aggregated euplankters forming the diurnal DZX, and the rise of interzonal species from the planktostad to their nocturnal layer depths within the euplankton. A nocturnal deepening of DZX does not, therefore, necessarily imply nocturnal sinking of any individual plankters, for it may be due simply to the layering of interzonal species at night deeper than daytime DZX.

The preferential aggregation of zooplankters at any particular depth may be a response to a favourable feeding situation at that depth, or to their crowding against a barrier or constraint imposed by the physical or chemical environment. Though the first possibility seems *a priori* to be the more likely in the present profiles, both are now examined.

Constraint is only likely to be caused by density, because it has already been suggested that other possible constraints (light, oxygen) are inoperative even in the case of DPS which lies deeper, and so more under their possible influence than is DZX.

#### Density

The zooplankton maximum occurs very close to D1 in all strata, the overall mean value of CZX being  $5 \pm 3.3 \text{ m}$  shoaler than D1; the difference DZX-D1 is not significantly different from zero ( $P < 0.05$ ) for the whole data pool and for all separate strata with the single exception of daytime profiles in very low latitudes in Regions IV and V; some anomalously deep values for D1 in this area, especially where mixed layers are relatively difficult to interpret in the equatorial divergence cell, caused the mean difference for this stratum to be  $\text{DZX} = \text{D1} - 20 \pm 5.6 \text{ m}$ . The linear regression DZX/D1 shows very significant covariance ( $P < 0.001$ ). Thus, the layer of maximum zooplankton abundance within the euplankton generally occurs some 50 m shoaler than DPS, and is very closely associated with the bottom of the mixed layer.

The aggregation of zooplankton at density discontinuities has recently been reported by

BOYD (1973) using an electronic particle counter, although the cause of the phenomenon remains obscure. Two possible explanations suggest themselves: firstly, that it may be a simple physical effect of the changed sinking rates to which any sinking particle will be subject at D1 or, secondly, it may be the result of an active food-seeking process. That the zooplankton profiles are not consistently skewed downwards towards DPS suggests that the physical process alone is not the cause.

#### *Phytoplankton*

The data show that zooplankton aggregation frequently occurs rather close to the depth of maximum  $^{14}\text{C}$  uptake (DCX) and usually significantly shoaler than the depth of maximum chlorophyll-*a* standing stock (DCLX). In fact, the overall mean depths of zooplankton aggregation and maximum  $^{14}\text{C}$  uptake are so similar ( $\text{DZX} = \text{DCX} + 3 \pm 3.1 \text{ m}$ ) that the difference between them is not significant ( $P < 0.001$ ); correspondence is closer at night than by day, when marginally significant differences do exist. Surprisingly, the linear regression  $\text{DZX}/\text{DCX}$  is not significant (Table 2); this may be because the mean depth difference is so small, or because night data for DCX were derived from the nearest day station (p. 740). Because DZX and DCX coincide so closely, DZX lies above DCLX by about the same distance as does DCX: the mean difference is  $\text{DZX} = \text{DCLX} - 20.5 \pm 3.5 \text{ m}$  ( $P < 0.001$ ) and significant difference is maintained for all strata of the data (Table 3); furthermore, in this case the two variables show a high degree of positive correlation ( $r = 0.294$ ,  $P$  0.01 to 0.001).

This suggestion that zooplankters tend to aggregate in depths of actively dividing (high  $^{14}\text{C}$  uptake) phytoplankton in preference to depths where less actively dividing (or low  $^{14}\text{C}$  uptake) but more abundant phytoplankton occurs has important implications for the interpretation of the form of phytoplankton profiles to which we shall return later (p. 749); previous detailed correlations between animal and plant plankton

profiles have suggested a rather different coincidence. ANDERSON, FROST and PETERSON (1972) and MULLIN and BROOKS (1972) have shown a correlation at three stations off Oregon and six off California, respectively, between maximum numbers of copepods and chlorophyll-*a* maxima in the mixed layer. HOBSON and LORENZEN (1972) at about 70 stations in the Gulf of Mexico, the Benguela Current and in the North Atlantic at 35 to 42°N, found a coincidence between chlorophyll-*a* maxima, microzooplankton (Lugols iodine samples) and pycnoclines. Unfortunately, neither of these sets of observations included  $^{14}\text{C}$  uptake data, in the absence of which it is impossible to be sure that the conclusions reached would not have been different had all three sets of data been available.

In all EASTROPAC regions, the phaeopigment maximum (DPHX) was deeper than DCLX, as expected (e.g. YENTSCH, 1965; LORENZEN, 1967), by about 20 to 30 m so that its depth is much greater than that of DZX ( $\text{DZX} = \text{DPHX} - 49 \pm 4.4 \text{ m}$ ), the area of presumed highest rate of production of these pigments during the grazing process. It seems probable that the closer coincidence of DPHX with DPS, which is only slightly, though significantly, deeper is not functional and that both variables are likely to be independently related to the lower part of the pycnocline where sinking rates of both plant cells and faecal pellets will decrease.

Also occurring in close proximity in all regions to DPHX is the shallow  $\text{NO}_2$  maximum (DNOX), an indicator of the depth of maximum remineralization of organic material by herbivores and heterotrophs (WADA and HATTORI, 1971); DNOX usually lay well below DZX (Table 1) and though within the depth range of the epiplankton is clearly unrelated to the depth of maximum zooplankton abundance but rather to the depth of aggregation of faecal material and senescent plant cells where microbial remineralization processes are most active.

These observations on the relations between DZX, density features and phytoplankton in the general zooplankton profiles can be, to a limited

extent, extended by the data from the special sorting categories.

Of the six such categories which always occurred in their maximum abundance within the euplankton (the genera *Euchaeta*, *Candacia*, *Acartia*, *Eucalanus*, *Lucifer* and *Stylocheiron*) only the last taxon showed important diel migration (mean 38 m). The nocturnal layer depth of *Stylocheiron* and the 24-h layer depths of the other taxa occurred very close to DZX and, thus, to DCX (Tables 1 and 4).

Despite this general coincidence with DCX there are individual deviations: the discrete layers of these six taxa lie with rather specific inter-relationships (Table 4). Thus, *Lucifer* lies in a relatively narrow layer (mean vertical range only 25 m by day), and shoaler (Table 4) than the copepods *Candacia*, *Euchaeta* and *Acartia* which lie closer to DZX; *Eucalanus* lies rather deeper (day mean 40 m) and *Stylocheiron* deeper yet

(day mean 71 m). Since each of these taxa, with the probable exception of *Lucifer*, comprise several species, it has to be assumed that the euplankton is composed of very many overlapping specific distributions, information upon which was not obtained from the samples though it was contained there: 21 profiles from EASTROPAC cruise 12 were analysed by Bruce Frost for six species of *Clausocalanus* (p. 731) and show how several co-occur at stations frequently and abundantly, but have specific layer depths and migration patterns. Three species (*C. parapergens*, *C. jobei* and *C. arcuicornis*) occur in daytime in the planktostad and lower part of the planktocline (mean daily depths of maximum abundance 170, 79 and 85 m, respectively) but rise at night to different levels within the euplankton (49, 54 and 40 m). On the other hand, *C. furcatus*, *C. minor* and *C. mastigophorus* occur in their greatest abundance very shoal in the day-

Table 4. Mean depths (m) of the abundance maxima of the main layers of specially-sorted taxa, of the daytime vertical extent of these layers, of their range of vertical migration and of their residual layers for all regions combined.

	LAYER DEPTHS				RESIDUAL LAYER DEPTHS	
	Day	Night	Extent	Range	Day	Night
<b>EPIPLANKTON TAXA</b>						
<i>Eucalanus</i> spp.	40	44	78	+4	-	-
<i>Euchaeta</i> spp.	28	17	50	-11	-	-
<i>Candacia</i> spp.	23	30	73	+4	-	-
<i>Acartia</i> spp.	23	10	84	-13	-	-
<i>Lucifer</i> spp.	19	17	42	-2	-	-
<i>Stylocheiron</i> spp.	71	33	56	-38	-	-
$\bar{x}$	34	25	63	-9	-	-
<b>INTERZONAL TAXA</b>						
<i>Rhincalanus cornutus</i>	229	19	173	-205	30	186
<i>R. nasutus</i>	300	30	74	-270	47	267
<i>Pleuronamma gracilis</i>	206	20	62	-186	40	267
<i>E. abdominalis/ziphius</i>	305	38	63	-272	30	100
<i>Euphausia diomedea</i>	372	16	59	-305	30	100
<i>E. azimia</i>	302	17	102	-285	22	100
<i>E. gibboides</i>	205	29	50	-276	70	120
<i>Nematoscelis gracilis</i>	283	57	22	-226	13	-
<i>Nematobrachion flexipes</i>	315	70	26	-275	17	110
<i>Eucalanus bungii</i>	301	108	56	-134	-	-
$\bar{x}$	289	33	91	-255	33	136

time (12, 21 and 10 m) apparently sinking at night, the mean day-night difference being about 28 m.

Obviously, the nocturnal migration of interzonal species upwards into the euplankton must cause a major shift in the vertical balance of biomass and numbers of individuals. To test this, progressive integrations were performed from the surface to 500 m, or to the bottom of the profiles if shoaler, for a number of the most important sorted categories: biomass, numbers of copepods, euphausiids, chaetognaths, pelagic fish, *Rhinocalanus cornutus*, *R. nasutus*, large and small *Pleuromamma* species (mainly *P. xiphias*, *P. abdominalis* and *P. borealis*, *P. gracilis*, respectively). From these step-wise integrations it was possible to calculate the percentages of plankton above and below any given level, and hence the relative amount in the euplankton. Table 5 shows that about 18% of the total biomass above 500 m was transferred from the planktostad to the euplankton at night by migration of interzonal species.

Surprisingly, the copepod data show that less than 10% of all individuals down to 500 m participated in this translocation and added relatively small numbers to the very abundant small euplanktonic species which, in all regions, comprised from 60 to 80% of all copepods above 500 m. The largest part of the nocturnal increase in euplankton biomass is derived from migrant euphausiids and small mesopelagic fish, though these are much fewer in number.

Table 5. Percentages of certain categories of plankton above 500 m which move into the euplankton from the planktostad at night.

Category	I	II	III	IV-VI	VII
Biomass	20	11	7	5	11
Total copepods	9	15	11	—	21
Juvenile euphausiids	—	62	47	—	11
Adult euphausiids	77	26	53	41	12
Chaetognaths	—	10	1	—	—
Adult fish	18	38	43	27	10
<i>Rhinocalanus cornutus</i>	—	—	—	24	11
<i>R. nasutus</i>	17	—	5	10	21
<i>Pleuromamma</i> (large species)	71	—	48	6	10
<i>Pleuromamma</i> (small species)	24	—	14	54	11

Both juvenile euphausiids, in relation to adults, and small species of *Pleuromamma* in relation to large, show reduced contribution to the euplankton at night, in addition to lying shoaler in their daytime residence layers within the planktostad. Of the groups examined in this way, chaetognaths show the least consistent pattern of nocturnal reinforcement of the euplankton, the data indicating a more scattered dispersal.

#### Presence of near-surface maximum

In 38 of the 86 profiles, it was possible to identify a near-surface zooplankton maximum separated by a minimum from the main body of the euplankton below (p. 737). The depth of this minimum (DZN) usually occurred between 10 and 20 m with a day-night difference (< 2 m) insignificantly different from zero.

There was variability in the frequency of occurrence of DZN both spatially and temporally. Most importantly, it was more frequent (50%) in daytime than at night (36%); this is evidently the effect of nocturnal shoaling of DZX and the consequent difficulty of separation of surface and subsurface maxima within the euplankton.

In Regions I to III, where D1 is moderate, DZN was identified in the highest proportion of profiles, occurring in 22 (= 63%). Rather frequently in Regions IV and V, and especially at those stations most influenced by the equatorial divergence, the only maximum occurring within the euplankton was very shoal and lacked the minimum above it: DZN was identified here in only 13 profiles (34%). This can best be interpreted as the result of the surfaceward displacement of DZX by the shoaling of the density parameters of the water column. In Regions VI and VII only three profiles (23%), none of which was in the gyral conditions of Region VII, included a subsurface minimum, presumably in response to the very great depths of the mixed layer and of DPS, and the very low plankton abundances, so that any aggregation within the euplankton was hard to detect.

The chlorophyll-*a* profiles rather frequently (in 51 cases of the 86 examined) showed evidence of a secondary pigment maximum very close under

the surface, generally no deeper than 10 m. In Regions IV and V, within the influence of the equatorial divergence and where a very high percentage of zooplankton profiles showed near-surface maxima, less than half of the profiles included such pigment maxima, perhaps indicating the grazing effects of 'surfaced' zooplankters.

#### LAYERING OF INTERZONAL SPECIES

The analysis of interzonal species was concerned with three components of the plankton: the deep, non-migrant taxa, the shoaler daytime layers of diel migrants, and the nocturnal layers within the epiplankton of diel migrants from the planktostad.

#### *Layering within the planktostad*

The layers of relatively abundant interzonal plankton that occur within the low-biomass water of the planktostad may form narrow strata only several tens of meters deep, or as rather thicker, more diffuse strata. The thin layers are distributed throughout sampled depths in the EASTROPAC material, while the thicker layers occur at rather constant depths and apparently in a rather constant relationship with sonic scattering layers. The upper and lower limits of the main layer at the 39 stations at which it was identified were from 226 to 330 m at daytime stations, and 227 to 349 m at a very few night-time stations: thus, in general, it extends for rather more than 100 m below a very consistent depth of about 225 m.

Both this main, thick layer of interzonal species and the bottom of the epiplankton can be correlated in about two-thirds of the daytime stations with the records from a 30-kHz echo-sounder which was operated continuously on high gain between stations. At each LHPR station the echogram was examined in detail, using the scale-expansion capabilities of the instrument to investigate the extent to which DPS, and the top ( $D'$ ) and bottom ( $D''$ ) of a layer of interzonal organisms could be recognized on the expanded echograms. This showed that there is a 70% probability that an echogram will predict DPS with a precision of  $\pm 15$  m, a 64% probability for  $D'$  and a 52% probability for  $D''$ ; that the

probability decreases with depth of the feature predicted does not necessarily imply increasing layer-diffusion with depth, and is probably due to the effects of signal attenuation over longer sound-paths. It is reasonable to suppose that DPS and (at least)  $D'$  were monitored in an approximate manner by the 30-kHz underway echograms taken throughout EASTROPAC and Fig. 5 shows echograms at 112 and 115°W in February to March 1967 which, compared with Fig. 4, considerably expand the description of the main features of the migrating layers within the planktostad.

Figure 5 shows that, while there is a good deal of small-scale variability in the depth of features within regions, there is remarkably little consistent variability between regions except at the southernmost end of the lines in Regions VI and VII, where the consistent deepening confirms the data shown in Fig. 2. The EASTROPAC data do not permit us to examine light levels at  $D'$ , which is considerably deeper (mean factor,  $\times 3.3$ ) than the depth of the euphotic zone though there is no simple correlation between these variables: many different species form the DSLs (see below) so perhaps a simple correlation is not to be expected.

However, DSL depths are well-known to be photo-regulated (e.g. BODEN and KAMPA, 1967) and light penetration in these oceanic areas where all turbidity is of biological origin (p. 740) is probably more uniform than most other variables in the water column which determine layer-depth.

Of the minor sorted categories of organisms, nine taxa (including seven single species), are interzonal diel migrants (Table 4); together with bathypelagic fish (principally the myctophid lanternfish *Diogenichthys* spp. and the gonostomatiid lightfish *Vinciguerria* spp.) these nine taxa comprise the bulk of the diel migrants in the samples.

As the table shows, most of the interzonal taxa had daytime layer depths, coincident with DSL depths, of between 250 and 300 m, and most layers were less than 100 m thick. The anomalous layer thickness shown for *Euphausia eximia* is largely influenced by a single station (76158) in the south equatorial current at which this species

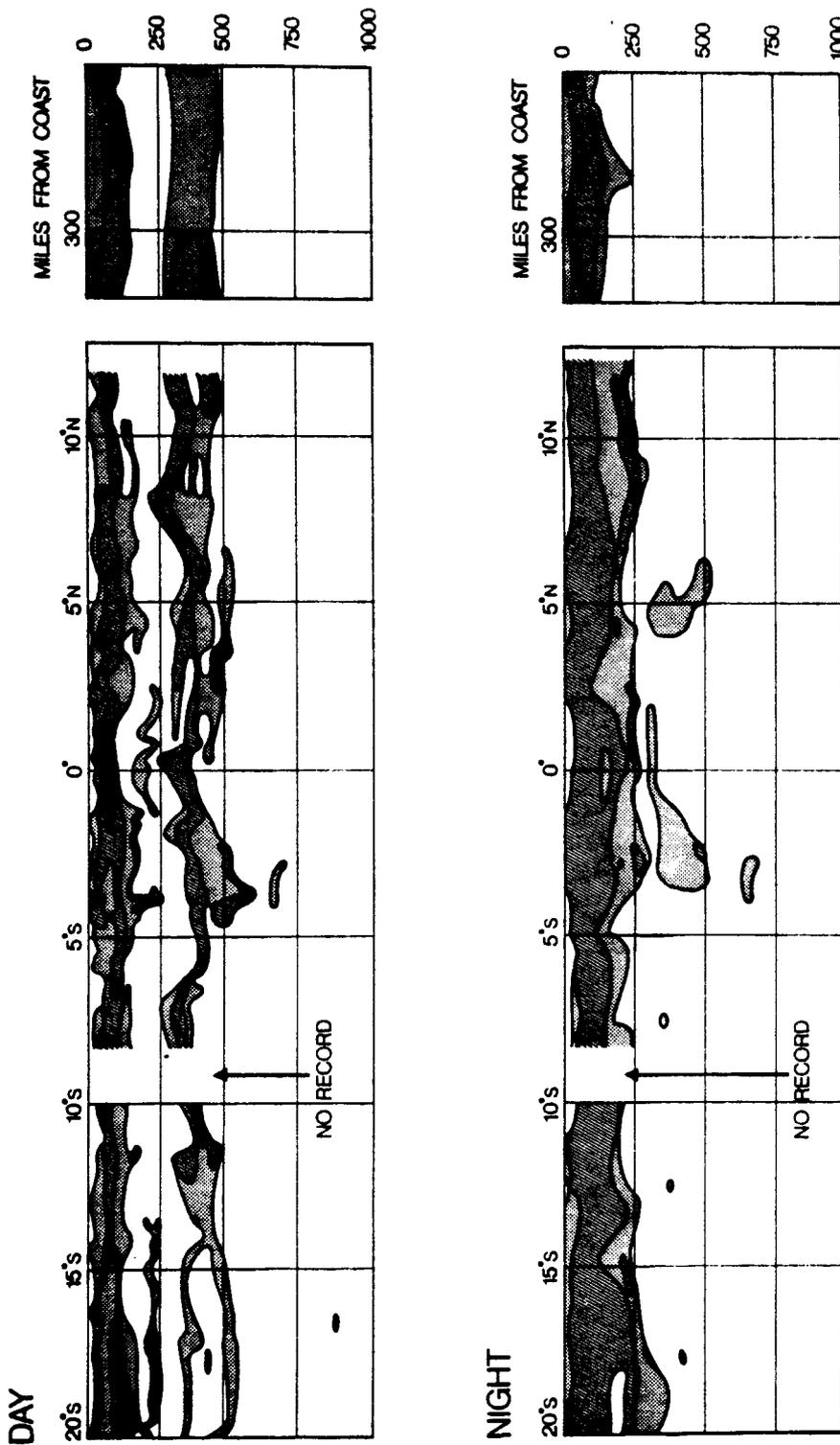


Fig.5. Sections of sonic scattering layers at 112°W and along a line from 12°N 112°W to the Mexican coast on the same scale. Contoured at 3 arbitrary levels of signal strength, in addition to 'no signal return'.

occurred in large numbers down to about 300 m without any layering.

As with the relatively non-migratory epiplankters, so the layer depths of the interzonal species do not coincide: *Euphausia eximia* and *Nematoscelis gracilis* regularly lie shoaler in the daytime than do the other species of euphausiids. *E. diomediae*, which generally lies deeper than any other euphausiid in daytime, also performs the greatest migrations and lies shoalest at night. PONOMAREVA (1963) confirms that this last euphausiid occurs very deep in the daytime in low precision opening-closing net hauls; she found maximal numbers at 200 to 500 m, but stragglers down to 1500 m.

The large species of *Pleuromamma* (*P. xiphias*, *P. abdominalis*) regularly lie deeper than the smaller species (*P. gracilis*, *P. borealis*), the latter occurring generally shoaler than 200 m; at night, however, the layer depths of the two groups of species are not so clearly separated. The large species of *Pleuromamma* were the most actively migrating copepods of the taxa examined in this study, occurring at night 250 to 300 m above their daytime levels.

Again, *Rhincalanus nasutus* and *R. cornutus* have mean daytime residence depths separated by about 75 m; compared with *Pleuromamma*, these are evidently much less consistent migrants, especially in the case of *R. cornutus*. Much more commonly than some other interzonal plankters, these species leave residual layers of individuals which fail to migrate both in the epiplankton in daytime and in the planktostad at night. ROE (1972a), indeed, found negligible diel migration in Atlantic forms of these two species off the Canary Islands in the SONDA data, as did VINOGRADOV (1968) in all regions except in the tropical divergence that occurs at the boundary between north equatorial and equatorial counter-currents, where he found a distinct nocturnal shoaling of the population. Thus, the occurrence of residual layers of non-migrant individuals more commonly in these species than is the case for *Pleuromamma* occasions no surprise.

Two main regional phenomena can be detected in the data for layer depths within the planktostad

and these are connected (1) with the thermocline shoaling at the equatorial divergence and (2) with the greater thermocline depth in the region of the southern summer thermocline.

Examination of individual station data shows that in the equatorial divergence in Region IV, the daytime layer depths of euphausiids remained generally deeper than 200 m at 8 stations, although at 10 others the daytime layers were shoaler than 50 m, even occurring in the upper 10 m; this occurrence of adult euphausiids at the surface was confirmed at several stations by actual observation (from the underwater ports of the bow-chamber) of red, adult euphausiids in large swarms. This was not an entirely passive reaction to water dynamics, for at each station not all euphausiids were surfaced, or normally deep; at 12100, for instance, *E. gibboides* remained centered at 320 m, while *E. diomediae*, *E. eximia*, *Nematoscelis gracilis* and *Nematobrachion flexipes* centered at 30 to 35 m. Similarly, among the copepods, at three of six stations in Region IV, both species of *Rhincalanus* and of *Pleuromamma* had layer depths at less than 30 m, mostly at less than 10 m, although at equatorial stations, part of the *Pleuromamma* population remained in daytime at depths exceeding 200 m.

In Regions VI and VII, to the south of the main stream of the south equatorial current, daytime layer depths of interzonal species as of the epiplankton, were greater than elsewhere in the survey. In almost every case, layer depths in VII were greater than in VI; at night, also, the tabulated data indicate that layer depths were deeper in these regions than elsewhere. These are the expected consequences of greater mixed layer depths and greater depths of features in the phytoplankton profile that have been discussed above, and are apparently unrelated to differential light penetration, which is remarkably slight (Table 1).

One interzonal taxon, *Eucalanus bungii*, which occurs deeper than all other sorted taxa, at depths in which black bathypelagic augapatalid copepods and scarlet hoplophorid carideans were beginning to occur in the sub-samples, does not appear to be a diel migrant; this species occurs

extremely deep in only a few samples and forms discrete layers at depths ranging down to 860 m. The most prominent layers of this species occur in the special deep samples (76197, 76202, 76158) in which strong layers occurred at 600 to 860 m, each being itself less than 100 m thick. This species shows indication neither of vertical migration, nor of equatorial shoaling, and clearly plays an unimportant role in the tropical pelagic ecosystem, yet *E. bungii* is a very important and abundant interzonal plankton in the northern North Pacific where it lies generally below 200 m and shows little diel migration (VINOGRADOV, 1968); in the California Current (LONGHURST, 1967) it is widespread below 300 m and evidently it is even further submerged in the EASTROPAC area through which it becomes progressively less frequent southwards (station occurrences: Regions I to III = 34%, IV and V = 27%, VI and VII = 15%).

#### Nocturnal layers within the euplankton

We have seen earlier (p. 741) that the layer of general plankton aggregation (DZX) lies very close to DCX and 20 to 30 m shoaler than the depth of the chlorophyll maximum; the data in Table 4 show that the depths to which individual taxa of interzonal migrants rise at night also correspond more closely to DCX than to DCLX. Thus, although the numbers of animals which participate in the diel translocation between the planktostad and the euplankton are not relatively great (p. 743), they do contribute to the general observed aggregation around DZX.

The migrant interzonal taxa for which data were acquired have mean nocturnal layer depths which range from 16 to 70 m (Table 4); only two species, *Nematoscelis gracilis* (mean 57 m) and *Nematobrachion flexipes* (mean 70 m) differ more than 12 m from mean DCX, and five species had their maximum abundances within 10 m of DCX at night.

As within the planktostad by day, so there is specific variation between layer depths of the interzonal taxa within the euplankton at night; among the four copepod taxa, those which lay deepest in the planktostad during the daytime

(*Rhincalanus nasutus*, *Pleuromamma abdominalis-xiphias*) lay deepest in the euplankton at night. The five species of euphausiids did not follow such a simple pattern, however, and the shoalest in the daytime (*Nematoscelis gracilis*) lay deepest at night. The most abundant euphausiid in the EASTROPAC area, *Euphausia diomediae*, regularly lay very shoal at night, having maximum abundances at less than 25 m in all regions.

ROE (1972b) showed quite clearly from the SONDA data for six species of *Pleuromamma* that the larger species lay deeper than the smaller during the daytime and his Fig. 8 shows some indication that the small species also lie relatively shoaler at night, but the EASTROPAC data reviewed here suggest that lack of vertical resolution in the SONDA samples (only five levels to 250 m) may have obscured the fine detail that evidently occurs within the upper 50 m at night.

#### CONCLUSIONS

The principal conclusions to be drawn from this study can be stated quite simply: zooplankton abundance is highest above the lower pycnocline and high biomass values rarely extend deeper than the layer of abundant chlorophyll; within this layer, both by day and by night, zooplankton tends to aggregate closer to the depth of maximum carbon fixation than to the depth of maximum chlorophyll standing stock. Finally, and perhaps less importantly, the presence of a near-surface enrichment of both animals and plants appears to have two possible causes: (i) extreme shoaling of the pycnocline which is associated with the shifting of biological processes close towards the surface, and (ii) an extremely stable mixed layer of moderate depth allowing the development within its upper few meters of a specialized neuston based on plant production processes which are probably to an extent isolated from those below.

Although several theoretical models which account for the general form of phytoplankton profiles have been published, these without exception include zooplankton grazing pressure as a constant, usually throughout the water column modelled. This could hardly be otherwise,

for only very few and very recent studies have investigated zooplankton-phytoplankton vertical relations in detail.

The model of STEELE and YENTSCH (1960) to account for the vertical distribution of chlorophyll, based on those of RILEY, STOMMEL and BUMPUS (1949), explains the observed chlorophyll distribution by the sinking of plant cells; accumulation of cells is assumed to occur either in response to density discontinuities or to the decreased sinking rates of plant cells below the euphotic zone due to their changing physiology in the absence of light.

These models recognize two conditions: the very shallow chlorophyll maximum which occurs when a phytoplankton population is increasing exponentially, and a deeper chlorophyll maximum when the phytoplankton population reaches an approximately steady state, later in the summer in high latitudes. In the former case, the chlorophyll and gross photosynthesis maxima coincide; in the latter, the chlorophyll maximum occurs deeper than the photosynthesis maximum.

As BLACKBURN, LAURS, OWEN and ZEITSCHEL (1970) showed, EASTROPAC standing stocks of phytoplankton, zooplankton, micronekton and fish varied seasonally by a factor of less than two, a very small variability relative to high latitudes; moreover, except in the eastern EASTROPAC area, where no LHPR hauls were taken, and the seasonal cycle is strongest, there was no detectable lag between the seasonal maxima of phytoplankton and zooplankton. Blackburn's study, which is based on the most comprehensive time-series of data available for the low-latitude pelagic ecosystem, thus confirms the previous prediction of HEINRICH (1962) that producers and consumers of plant material should co-vary seasonally in the open tropical ocean. It further suggests that here one cannot expect to find the detailed coincidence in the vertical sense between maxima of chlorophyll-*a* and carbon fixation rate which can exist ephemerally in higher latitudes with greater instability in the seasonal production cycle. Thus the EASTROPAC profiles might generally be expected to approximate the summer chlorophyll profiles of much higher latitudes, and the

sections presented in the EASTROPAC atlases (LOVE, 1971) confirm that this is the case.

What is new in the LHPR profiles is the demonstration that zooplankton aggregation, and hence grazing pressure on plant cells, is strikingly non-uniform with respect to depth and concentrates closer to the depth of maximal plant production than to maximal plant material. It is hard to avoid the suggestion, therefore, that a causal relationship exists between the form of the profiles of herbivore and producers. That, in short, the form of the chlorophyll profile is influenced, or even determined, by a depth-differential in the grazing pressure of herbivores, in addition to the effects of differential sinking rates invoked in the earlier models.

Of course, not all the zooplankters profiled in this study were, in fact, obligate herbivores, nor did they comprise all the pelagic herbivores present in the water column. However, the numerical profiles are dominated by small copepods which are at most only one trophic level above the primary herbivores whose biomass is likely to be dominated by very small organisms, and hence it is reasonable to consider the plankton profiles studied here as dominated by herbivorous organisms. There is evidence that levels of maximum abundance of the microzooplankton, which in this region must be extremely important consumers of primary production, coincides at EASTROPAC stations with DZX as determined in this study (e.g. BEERS and STEWART, 1971). It seems unlikely that the larger organisms of the micronekton (BLACKBURN, LAURS, OWEN and ZEITSCHEL, 1970) contribute importantly to herbivore grazing pressure, so it seems reasonable to equate LHPR-plankton in this region with herbivore distribution.

An hypothesis similar to that put forward here has already been proposed by LORENZEN (1967) on the basis of a small number of LHPR stations, at which phytoplankton profiles were also obtained, off Baja California. Further, VERRICK, MCGOWAN and MANTYLA (1973) have suggested that differential zooplankton grazing from animals concentrated above the chlorophyll maximum layer in low latitudes may help to

maintain a sharp gradient above it, but propose that the deep chlorophyll maximum is ultimately determined by the nutrient regime. Such suggestions are an advance on the earlier models discussed above which depend on decreased sinking rates of plant cells, but the hypothesis has yet to be tested directly to validate the relationship which could be demonstrated in the EASTROPAC data only in a statistical sense; direct validation depends on simultaneous and matched high precision profiles not only of plant pigments and zooplankton but also of plant production rates. So far as I am aware, production profiles of the required precision have not yet been made.

The grazing hypothesis also raises the question of why additional grazing pressure does not develop deeper than DZX, where the chlorophyll profile suggests that food availability for grazing organisms is higher than at DCX. Why do the interzonal herbivores traverse the chlorophyll maximum in their nocturnal rise (p. 742), to seek depths where phytoplankton biomass is apparently always lower?

Two possible answers suggest themselves: firstly, that the phytoplankton population at the chlorophyll-*a* maximum is physiologically and biochemically less attractive as a food source than the plant cells at the depths of maximum gross photosynthesis or, secondly, that the other factors presumed to determine the rate and extent of diel migration, and of residence depth of non-migrants—light and temperature—over-ride the selection of the depth of maximum chlorophyll.

Certainly, the plant cells in the photosynthesis maximum (DCX) differ biochemically from those deeper (e.g. JEFFREY, 1974) and actively dividing cell populations will contain a higher proportion of larger pre-division cells which have been shown to induce increased feeding rates in a calanoid copepod (RICHMAN and ROGERS, 1969); the deeper cells are senescent, may not be actively dividing, and may be less attractive to herbivorous plankton. On the other hand, one must be impressed by the rigidity of migrant plankters' response to light intensity (e.g. BODEN and KAMPA, 1967; BACKUS, CLARKE and WING, 1965) which simply may not permit sufficient flexibility

of response for zooplankton grazing pressure to develop on plant cell concentrations at whatever depth these may be encountered.

The general hypothesis that there is a relationship between the nature of zooplankton profiles and the vertical distribution of density and phytoplankton production is now examined in the light of regional and seasonal differences within the EASTROPAC area.

It is in Region I that plankton profiles (Fig. 6) most frequently show all major characteristics of the euphotic zone, and this is clearly related to the isothermal mixed layer defined by an extremely sharp thermocline. In general, D1 is here sufficiently deep for the development within the mixed layer of a sub-surface zooplankton maximum separated from a surface maximum and this is associated with the development of characteristic phytoplankton profiles.

As expected, DZX shoaled in the second half of the year to about half its mean depth for February to March but, despite this crowding surfaceward by the shoaling of D1, the zooplankton profiles retained their typical form; very high zooplankton volumes occurred near 100°W in cruises 30 and 60 in relation to doming off Costa Rica. Even though tunicates and coelenterates were unusually abundant in these profiles (especially 30254) their essential profile-form remained typical of the region.

Only four stations were occupied in the north equatorial current in Region II, one in February to March 1967 and three in the December to January following: these are insufficient to characterize the plankton profiles in this region, but give no evidence of being significantly different from those characteristics of Region I.

Because of its seasonal occurrence in the study area (p. 732) profiles were obtained from the north equatorial counter-current (Region III) only in the second half of the year and these showed D1 to be much shoaler than in Region I to the north of the thermocline ridge marking the northern boundary of the north equatorial counter-current. Related to this, the zooplankton profiles frequently showed no separation between surface and subsurface maxima within the

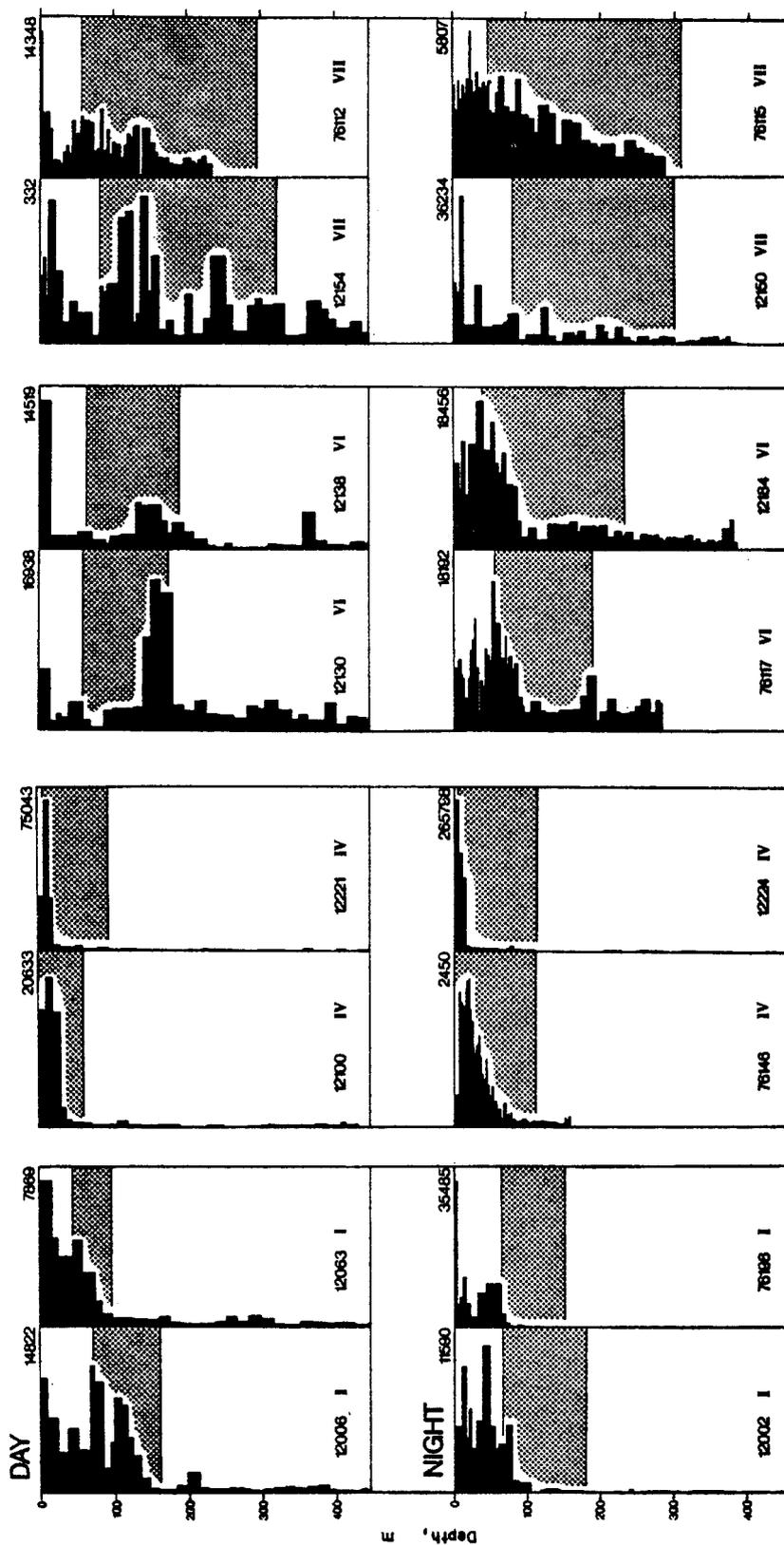


Fig. 6. Two exemplary profiles for each of four regions (I, IV, VI and VII) by day and by night, to show main characters of typical profiles of these regions; the thermocline, as indicated by depth interval between D1 and D2, is stippled. Maximal numbers of organisms ( $100 \text{ m}^{-3}$ ) are indicated above each profile.

epiplankton, and mean DPS was shoaler than in Region I.

In the second half of the year in Region IV the very strong vertical eddying as the equatorial under-current surfaced resulted in a relatively cold and deep mixed layer, which was reflected in the distribution of the main features of the epiplankton; however, early in the year when D1 is less than 10 m, the epiplankton extends relatively deeper into the thermocline than in regions with moderate depths of D1 (Fig. 6). The ratio DPS/D1 for Regions I, II, III and V ranged from 1.7 to 3.8 for all seasons; in Region IV, however, it was 3.5 in June to July when the thermocline was deepest, but reached 9.6 in December to January and 45.8 in February to March when the thermocline was shoalest. This confirms that in extreme conditions of shoal thermoclines, the apparent lower limiting depth of the epiplankton responds principally to some factor other than density, for which there is no discontinuity at D2; the difference in depth between DZX and DCX remains relatively slight at all seasons in this region despite the important variations in D1, suggesting that under these very unusual conditions the link between plants and animals is greater than that between either and density.

Values for D1 in Region VI are intermediate between those in Regions I to III and V to the north and the greater depths in VII to the south, and the decreased mixed layer stability in VI implied by the step-wise temperature profiles above D1 is apparently reflected in the zooplankton profiles which here mostly do not include a subsurface minimum (Fig. 6); the existence of a depth zone of relatively sparse plankton in the upper part of the epiplankton is evidently a characteristic of regions with a thermostad above D1. Most profiles in Region VI have a simple subsurface maximum within the epiplankton or else a relatively complex system of maxima which are usually rather obviously correlated with density features (Fig. 6). The profiles of chlorophyll-*a* and carbon fixation are not sufficiently detailed, however, to demonstrate similar correlations with density.

To the south of 14°S, in the gyre proper where south Pacific central water characteristics occur, stations were worked in Region VII only in February to March, in the southern summer. These zooplankton profiles (Fig. 6) are mostly unlike those at any other stations in the EASTROPAC area; daytime profiles from 8 to 14°S have a very shoal surface maximum and several discrete subsurface maxima, commonly at depths exceeding 100 m, while in the southern gyral water the profiles were composed of almost uniformly low zooplankton densities from the surface to the greatest depths sampled. At night from 8 to 14°S, nocturnal migration upwards resulted at several stations in relatively heavy plankton densities from the surface to a planktonicline at less than 100 m depth.

Because neither DZX nor DCX could be as well defined as in more northerly regions, and because DCLX was apparently often located deeper than chlorophyll sampling was carried, the relationship between plant and animal profiles appeared to be relatively loose here. This may well be a result which is more apparent than real, however, and to some extent is certain to be a reflection of the inadequacy of the standard EASTROPAC sampling protocol under these conditions.

This analysis of the EASTROPAC data suggests a generalization which may be extrapolated to other areas of the ocean: in fact, to wherever the phytoplankton profile includes a chlorophyll maximum which underlies a primary production maximum. VENRICK, MCGOWAN and MANTYLA (1973) review deep (< 100 m) chlorophyll maxima in the Indian Ocean, the Sargasso Sea, the Gulf of Mexico and the northwest Pacific, and their own data show that one extends from 80°W to 180°E and from 45°N to 25°S in the Pacific Ocean. The EASTROPAC data suggest that the chlorophyll maximum is usually overlain by the depth of the maximum rate of primary production, itself probably corresponding to the depth of maximum photosynthetic rate per unit of chlorophyll (ICHIMURA, 1956).

In higher latitudes this pattern occurs only for a few weeks or months each summer, as STEELE

and YENTSCH (1960) have suggested and as ANDERSON, FROST and PETERSON (1969) have shown off Oregon at about 45°N. In areas of strong divergence or coastal upwelling it cannot be expected to occur at all, as is seen in the EASTROPAC profiles off South American (LOVE, 1971), and in the Somali Current profiles published by YENTSCH (1965). Not only does the instability of the water column in such places preclude the establishment of the relationship postulated here, but also strong seasonal vertical migration occurs in the zooplankton. As in high latitudes, where the zooplankton profile in winter is quite different from those observed in the present study due to deep over-wintering populations of sub-adult copepods (e.g. VINOGRADOV, 1968), in intermittent low-latitude upwelling situations the same may occur in the interstadial (LONGHURST, 1967). Under such circumstances the vertical distribution of grazing pressure must be quite different from that in stable water columns in the EASTROPAC area.

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